

ORNITHOLOGICAL LITERATURE

REVIEW: Three papers on variation in flickers (*Colaptes*) by Lester L. Short, Jr. 1965a. HYBRIDIZATION IN THE FLICKERS (*COLAPTES*) OF NORTH AMERICA. Bull. Amer. Mus. Nat. Hist., 129:307-428. 1965b. VARIATION IN WEST INDIAN FLICKERS (AVES, *COLAPTES*). Bull. Florida State Mus., 10:1-42. 1967. VARIATION IN CENTRAL AMERICAN FLICKERS. Wilson Bull., 79:5-21.

These three papers represent the fruition of Short's extensive research on flickers begun in 1955 at Cornell University under the supervision of Charles G. Sibley. The main analysis is of 6,000 specimens which resulted from field work by Short and many others in critical areas of contact between phenotypically well-differentiated forms in the Great Plains and in Arizona. The studies of West Indian and Central American birds were based entirely on museum specimens and pertinent literature; the need for field work on the ecology and behavior of the flickers of these areas is stressed.

In the major paper, the genus *Colaptes* is broadened to include as subgenera the currently recognized genera *Chrysoptilus* (three species in South America) and *Nesocelus* (one species in Cuba), as well as *Colaptes* (North and Central American flickers) and *Soroplex* (three species in South America), the latter two subgenera having comprised the genus *Colaptes* in the sense of Peters (Birds of the world, 1948, vol. 6).

Short derives "the ancestral North American flicker" from South America via Nicaragua and Central America, a notion supported by the fundamental diversity of the enlarged genus *Colaptes* in South America, where also the genus *Piculus* (said by Short to be closely related to *Colaptes*) has radiated. Short feels that all North American flickers belong to one species, *Colaptes auratus*, divided into five subspecies groups: the *mexicanoides* group, including two subspecies in Central America; the *cafer* group, including five subspecies in Mexico and western North America; the *chrysoides* group, including four subspecies in the southwestern United States and northwestern Mexico; the *auratus* group, including two subspecies in eastern and northern North America; and the *chrysocaulosus* group, including a subspecies in Cuba and a subspecies on Grand Cayman Island. The subspecies *borealis* of Ridgway, *canescens* of Brodkorb, *chihuahuae* of Brodkorb, *martirensis* of Grinnell, and *sedentarius* of van Rossem are not recognized in the major paper. Later (1967) Short provides evidence for the submergence of one of the subspecies of the *mexicanoides* group, *pinicolus* of Dickey and van Rossem. Although Short does not explicitly make this point, it is convenient to view the five subspecies groups as falling into three categories:

- I. The *mexicanoides* group plus the *cafer* group (= "Red-shafted Flickers")
- II. The *chrysoides* group (= "Gilded Flickers")
- III. The *auratus* group plus the *chrysocaulosus* group (= "Yellow-shafted Flickers")

Indeed, these categories probably represent separate evolutionary trends from the original stock that invaded North America, and they are the "species" of much modern literature, including the A. O. U. Check-list of North American birds, 1957.

In a convincing interpretation, *chrysoides* is said to have evolved from either a pre-*cafer* (p. 404) or an early *cafer* (p. 412) population in Baja California. *Chrysoides* later spread north, east, and then southward along the coastal plains of northwestern Mexico. In the opinion of the reviewer, the ability of *cafer* stock to give rise to *chrysoides* has great significance, to be discussed further below. The possibility that *auratus* stock evolved from *cafer* or pre-*cafer* populations after spreading from the west in North America

seems entirely logical on zoogeographic grounds. Short did not discuss this point but indicates that he plans to do so in the future (1967:19).

Cuban *chrysocaulosus* is derived from *auratus* by invasion from Florida, perhaps in the early Pleistocene. Evidently later, in the mid- to late Pleistocene, *chrysocaulosus* stock reached Grand Cayman Island from Cuba and evolved into *Colaptes auratus gundlachi*. *Chrysocaulosus* probably arrived in Cuba after *Colaptes fernandinae*, which had already pre-empted the ground-foraging niche and thereby "forced" *chrysocaulosus* into a more arboreal role, a situation worthy of close examination by both the ecologist and anatomist. Short's notion of a similar, though earlier, northern origin for the peculiar *fernandinae* is less appealing. By his own admission, *fernandinae* "resembles South American flickers of the subgenera *Soroplex* and *Chrysoptilus* more closely than it does *Colaptes auratus*." Rather, evidence suggests a South American origin for *fernandinae* from old *Colaptes* stock not necessarily involved in the ancestry of the subgenus to which *auratus* belongs.

The most penetrating treatment is afforded the populations from the long zone of contact between *cafer* and *auratus*, from British Columbia to Texas, where interbreeding is apparently free. In a narrow zone where only hybrids are present there were no signs of behavioral isolating mechanisms. However, because "pure" forms of *cafer* and *auratus* are not in contact, their possibly divergent behavior in pairing could not be seen in the hybrid zone, especially if hybrids are at an advantage there over pure parental types. The analysis of the several contacts in the plains is carefully documented; especially well studied were the series of samples taken at intervals along a transect following the Platte River Valley in Nebraska and Colorado. Short acknowledges his considerable debt to Dr. Frederick Test who permitted his use of much unpublished material in the form of specimens and notes from Test's extensive work with flickers years ago at the Museum of Vertebrate Zoology and in the field in Montana. Special analysis properly given to 15 mated pairs obtained in Montana by Test and his associates revealed no clear indication of mating preference. Even the hardest splitter should now be convinced of the conspecificity of the two forms. Particularly commendable in the section on hybridization in the plains is the format of presentation of detailed data, often from single specimens, which affords the reader a level of examination not often permitted when diverse samples are pooled improperly. Flickers representing *cafer* and *chrysoides* were also studied in the field in Arizona, where the situation is much different from that in the plains. *Cafer* is basically an upland bird; *chrysoides* reaches its greatest density in the lowland and foothill saguaros, but occurs also in cottonwoods in canyons at the bases of mountains. Pure populations of *cafer* and *chrysoides* are not in contact except through one intervening hybrid population along the Agua Fria River and its tributaries. The "barrier is the grassland and open oak-juniper woodland generally found between lowland cactus desert and upland pine-oak woodland," where neither flicker can breed because of the lack of nesting sites. In the virtual absence of contact of the two forms I find weak Short's hypothesis (p. 377) that the geographic range of *chrysoides* is being limited by *cafer*. Strong differences in temperature and humidity tolerances, among other habitat requirements, are more probable reasons for the essential allopatry of their ranges.

Five other small and widely scattered hybrid populations were studied in addition to that along the Agua Fria River. Each is isolated from other hybrid populations and from parental stock. No two hybrid "swarms" are alike; they vary in degree of intermediacy toward one or the other parental type in expression of the various characters, evidently thereby reflecting response to local selective forces. Short's detailed discussion

of habitats and possible avenues of gene flow in regions where *cafer* and *chrysoides* occur in close proximity is particularly excellent. The small samples of specimens from the limited areas of hybridization were thoroughly analyzed, with statistical treatment where possible. However, the lack of similar statistical treatment of data on size variation for comparative samples of *cafer* and *chrysoides* (Table 34) away from the hybrid areas renders difficult their interpretation.

Evidently contact between *cafer* and *chrysoides* was more extensive in the past when riparian vegetation was more continuous because of higher water tables and less habitat destruction. Very little gene flow occurs at present between *cafer* and *chrysoides*; all but one of the variously intermediate populations are apparently stabilized and isolated. In view of this virtual lack of gene exchange and because of the strong discontinuities in size, color, habitat preference, and, undoubtedly, climatic tolerance between the huge populations of "pure" *cafer* and *chrysoides*, I am inclined to minimize the importance of their limited hybridization. Therefore, despite the great idealistic appeal of including all North American flickers in one species, I do not follow Short in grouping *chrysoides* with *cafer*, but instead favor the retention of the Gilded Flicker as a separate species. It is all too easy to judge the extremely limited *chrysoides-cafer* contact as being equivalent to that of *cafer* and *auratus* in the Great Plains and, with that situation of massive interbreeding in mind, improperly include *chrysoides* with *cafer*.

However, this point of difference in taxonomic philosophy should not obscure the fact of Short's excellent treatment of this problem in the gathering and analysis of specimen data and in the interpretation of possible contact zones, often through his own field exploration.

To analyze hybrids between the *cafer* group and the *auratus* group, Short uses a series of scores representing gradations for each of the following six color characters for males (five characters for females, which lack a strikingly colored malar mark): Crown color, color of ear coverts, throat color, nuchal patch, shaft color, and malar color. The gradations for throat color, for example, are "0," vinaceous tan, as in *auratus*; "1," gray traces, usually on lower throat; "2," mixed gray and tan; "3," tan traces, usually near chin; and "4," gray, as in *cafer*. The individual scores for each character are then summed, which results in a total score between "0" for a "pure" *auratus* to "24" for a "pure" *cafer*. In females the range is from 0 to 20. Similar sorts of indices have been used in other studies of avian hybridization.

The philosophy underlying Short's entire discussion is that traces in one population (population B, for example) of characters expressed routinely in another population (A), and presumably evolved when A and B were not in contact, means that genes from population A are infiltrating population B because of secondary contact. Thus, traces of a red nuchal mark in 25 per cent of Californian Red-shafted Flickers are interpreted as being a result of introgressant "red nuchal genes" from Yellow-shafted Flickers in the eastern or northern part of the continent. Also according to this philosophy traces of "*auratus*" characters (except shaft color) in *chrysoides* of southwestern North America are a result of introgression of genes for that character, originally from *auratus*, genes that passed through *cafer* to finally reside in *chrysoides*. The expression of the various phenotypes, thus concludes Short, "attests to the ability of populations of the three forms to partake of one another's genetic variability" (p. 406).

However appealing this explanation may be for certain situations of hybridization in birds, for the North American flickers I feel that Short's interpretation is incorrect, and that introgression is only reasonably invoked as the explanation for the variability close to the hybrid zones in the plains and in Arizona. Thus, it is misleading to term

the red nuchal mark an "*auratus* character;" rather it should be called a *flicker* character, lost in 75 per cent of *cafer* and in ? per cent of *chrysoides*, and present in 99+ per cent of *auratus*. Can we ignore the fact that a red nuchal mark occurs widely not only in most members of the genus *Colaptes*, but also in most members of the closely related genus *Piculus*, and indeed in a wide variety of other picids? Actually, the red nuchal mark is almost best termed a *picid* character in view of its wide expression in the family. The likely explanation for *most* of the occurrence of red nuchal traces, then, in *most* of the populations of *cafer* in western North America away from the hybrid zones, is that these traces have their genetic basis deep in the stock that gave rise to all flickers and their relatives, and that in certain forms (as in the *cafer* and *chrysoides* groups) the trait has been largely lost although it occurs even in these populations as an expression of *normal variation*, often in 25 per cent of the individuals (*cafer* and *mexicanoides* groups).

Short is aware of this problem when he writes (1965a:319): "Since it is impossible to separate effects due to introgression from those due to the genetic potential of *cafer* itself, a degree of error is incorporated in the use of this character [the nuchal mark] in the color analysis of hybrids. The magnitude of the error can be seen by an examination of the occurrence of nuchal traces in those forms geographically isolated from populations of the *cafer* group. These include the subspecies *rufipileus* of the *cafer* group, and *mexicanoides* and *pinicolus* [synonymized in the 1967 paper] of the *mexicanoides* group. The *chrysoides* group, as is shown below, is in genetic contact with the *cafer* group. There is introgression of genes determining the presence of the nuchal patch from the *auratus* group into the *cafer* group, and thence into the populations of *chrysoides*."

To continue Short's own line of reasoning, I believe that not only is the range of variation in extent of nuchal mark in the isolated *mexicanoides* a valuable yardstick by which to measure the extent of normal variability in *cafer*, but I would extend this to include the variation in the other five color characters in his hybrid index. Similarly, the normal variability in character expression in the isolated *chrysocaulosus* can be used as the standard against which can be measured the additional variability supposedly resulting from hybridization and introgression in the main groups of continental *auratus* (see below).

Short's own argument against use of this character is equally applicable to all of the other five color characters he used in his hybrid index. Like the traces of nuchal marks in far western *cafer*, traces of "*auratus*" ear covert color (in 23 of 74 specimens) and traces of "*auratus*" throat color (in 24 of 74 specimens) in populations of California and Oregon may have nothing to do with past hybridization; these traces can be interpreted as normal variability inherited from the ancestral gene pool. Furthermore, (1) the ability of *cafer* or pre-*cafer* stock to produce *chrysoides* with its yellow shaft color, and (2) the ability of *cafer* to produce *rufipileus*, independently, with its *chrysoides*-like crown color, and (3) in view of the simple genetic and dietary basis for the difference between red and yellow shaft colors in all flickers, and (4) the presence of red and black together in malar marks of *mexicanoides* are all additional points of evidence which demonstrate the degree of variability in North American flickers and provide arguments against any meaningful use of these characters as evidence for past hybridization and introgression *at any distance away from the hybrid zone*.

I believe that there is justification for re-interpretation of Short's hybrid index system as follows: Within a single character in the system (see 1965a:318, table 2) scores of 0 and at least some of the birds categorized as 1 are typical *auratus*, 2 is intermediate,

and at least some of the birds in 3 and all of those in 4 are typical *cafer*. Because the scores of 1 and 3 in each character very likely include variation normally within *auratus* and *cafer*, respectively, let's permit each "pure" type (0 for *auratus*, 24 for *cafer*) to possess traces of at least three of the six color characters Short attributes as having resulted from hybridization with the other form. This is quite conservative; variation may actually permit traces of all six characters in either normal *auratus* or *cafer*. Under this reasonable re-assessment of the index, then, when the scores are summed for totals, males indexed at 0 to 3 are *auratus* showing normal variation, birds indexed at 4 or 5 may be either normally variable *auratus* or they may be hybrids, birds indexed at 6 to 18 are definite hybrids, birds indexed at 19 or 20 either may be hybrids or they may be normally variable *cafer*, and birds indexed at 21 to 24 are *cafer* showing normal variation. According to this analysis the zone of hybridization in the Great Plains becomes narrowed to that region where the specimens show variability beyond the range normally expected, variation that can be interpreted justifiably as that resulting from hybridization and introgression. Thus in Figure 3 on p. 327, most of the individuals from Schuyler, to and including Sutherland, are probably normal *auratus* with some hybrids (one definite hybrid from Sutherland). Samples from Big Springs are hybrids toward *auratus*. Birds from Crook are hybrids. Birds from Fort Morgan and Greeley are hybrids toward *cafer*. Samples from western Colorado are mostly *cafer* with some hybrids. Importantly, data on size variation demonstrate clearly that the influence of true introgression occurs over a zone much narrower than Short proposes on the basis of color characters. In wing length, for example, only the sample from Crook is definitely intermediate between *cafer* and *auratus* (Table 5, p. 332), although the two samples geographically adjacent to the Crook sample would almost certainly show the influence of hybridization more clearly if more specimens were available.

As support for this interpretation I should like to cite Short's own valuable data on "character indexes" for *mexicanoides* (1967:17) and *chrysocaulosus* (1965b:21-22). In *mexicanoides*, character index values ranged from 19-23 in 87 males (mean \pm 2 S.E. = 21.46 ± 0.20). In *chrysocaulosus*, character index values in 35 males ranged from 0 to 3 (mean = 1.90 ± 0.22). In *auratus* of Florida, character index values of 37 males ranged from 0 to 3.5 (mean = 1.35 ± 0.36). My estimates above, based on the assumption that birds indexing at "21" to "24" are probably normal *cafer*, and that birds indexing at "0" to "3" are probably normal *auratus*, are thoroughly substantiated by the normal ranges of variation in these isolated populations.

One of the most striking revelations that came to me upon examining Short's generalized maps of the geographic distribution of flickers in North America is the great coincidence of phenotypic change in the various forms with major climatic boundaries on the continent. With this in mind one wonders to what extent the phenotypes reflect underlying genetic-physiologic adaptation to the general temperature and humidity regimes in the regions where they occur. The intermediate position of the hybrid zones in relation to the general climatic preferences of parental populations, in both the plains and in Arizona, suggests that there may indeed be positive selection maintaining hybrids in regions where neither parental stock is at maximal selective advantage. I find no discussion of physiologic adaptation in Short's papers and would merely stress here the need for experimental work along these lines.

Short mentions that a study of flicker behavior (in preparation) and a review of the literature "have failed to produce any evidence for the occurrence of major differences in behavior among the forms of flicker that hybridize." Hopefully the paper in progress will include the careful observations of close range interactions both between territorial

males and between mates needed to further elucidate the functions of the nuchal and malar marks in flickers. However similar the gross behavior of flickers may be, it seems unlikely that color differences in malar marks and presence or absence of nuchal marks in *cafer* and *auratus* are not accompanied by significant differences in behavior (head movements in appeasement situations, for example), regardless of whether these marks have anything to do with reproductive isolating mechanisms. One wonders, for example, if selection for the loss of the red nuchal mark in *cafer* was accompanied by simultaneous selection for the appearance of redness in the malar stripe. Admittedly, speculation about the evolution of these marks will be relevant only after meaningful data on their function are at hand, data which reveal the selection pressures operating to direct their evolution.

In summary, Short's meticulous analysis of phenotypic variation in the flickers of the North American hybrid zones and in the West Indies provides the evolutionist with a vast source of dependable material for interpretation. That there exist other plausible explanations for some of his findings should come as no surprise considering the complexity of the situation. His carefully gathered data set the stage for investigation of the numerous unsolved problems in the group. In addition to the need for further refined examination of phenotypic variation of populations in areas not well represented now by specimens (western United States, Mexico, and Central America), the most profitable lines of research on these readily available birds would seem to be in behavior (function of head marks, for example) and in comparative physiology (temperature and humidity tolerances and preferences of birds representing the various phenotypes).—NED K. JOHNSON.

WATERFOWL IN AUSTRALIA. By H. J. Frith. East-West Center Press, Honolulu. 1967: 6 × 9 in., 328 pp., 5 col. pls. many bl. and wh. illus., 19 distribution maps. \$10.00.

Our dearth of knowledge concerning Australian waterfowl has, until recently at least, been so severe as to once stimulate Ernst Mayr to write a paper (*Emu*, 45:229-232, 1946) reminding Australians how little was then known about their native waterfowl. The situation was especially serious in view of the fact that no fewer than six of Australia's 19 species of indigenous waterfowl represent monotypic genera that are largely or entirely restricted to that continent. Furthermore, these include such phylogenetically significant and taxonomically controversial genera as *Anseranas*, *Cereopsis*, *Malacorhynchus*, and *Stictonetta*, the last two of which have never been available for behavioral study outside Australia. In view of this, any amount of new information on Australian waterfowl must be enthusiastically welcomed; an entire book on the subject can only be regarded as a godsend.

H. J. Frith's studies on Australian waterfowl go back to the mid-1950s, when he discovered the interesting fact that several duck species of interior Australia have their breeding seasons timed by local water conditions rather than by photoperiod changes or other proximate factors. More recently he was placed in charge of the Division of Wildlife Research of the C.S.I.R.O., the governmental agency charged with conducting and integrating scientific research in Australia. This has placed him in the enviable position of organizing federally-supported research efforts related to waterfowl, and one of the fruits of this situation is the present book.

Unlike the recent monograph by Delacour, Frith has not resorted to the simple expedient of publishing extensive quotations of possible historical interest but dubious current value. Instead, each species is dealt with intensively, and the information on distribution and movements, habitats, and breeding biology are of particular value.